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THE EFFECTS OF SHELL SIZE AND SHAPE ON GROWTH AND FORM IN THE HERMIT CRAB *PAGURUS LONGICARPUS*

NEIL W. BLACKSTONE[1]

Department of Biology, Yale University, New Haven, Connecticut 06511

ABSTRACT

Pagurus longicarpus from two geographic locations were raised in the same environment in three species of gastropod shell. These shell species differed in shape and maximum size. Crabs in small, high-spired shells attained smaller sizes than those in large, low-spired shells. Further, the relative growth rates of male crabs showed differences related to shell differences. Males in small, high-spired shells produced relatively longer claws and greater right/left claw asymmetry than males in large, low-spired shells. These results show the close interaction between hermit crabs and utilized shells and may explain the geographic variation of *P. longicarpus*. Along the Atlantic coast, southern crabs are smaller and have relatively longer claws and greater right/left claw asymmetry than northern crabs. Southern crabs utilize small, high-spired shells almost entirely, whereas northern crabs utilize a high proportion of large, low-spired shells. Size and shape differences between geographic populations of *P. longicarpus* thus may be due to differences in inhabited shells.

INTRODUCTION

Hermit crabs are anomuran crustaceans which generally inhabit gastropod shells. This shell-living habit has resulted in the modification of many aspects of hermit crab biology (Jackson, 1913; Reese, 1969). Since shells are easily measured and manipulated and since they are a critical resource for hermit crab populations (Provenzano, 1960; Hazlett, 1970; Vance, 1972; Kellogg, 1976; Spight, 1977; Abrams, 1980; Bertness, 1980), research has focused on the hermit crab/shell interaction (see Hazlett, 1981). This interaction has many subtle ramifications. For instance, hermit crab body size and clutch size (and hence fitness) vary depending on the shell inhabited (Markham, 1968; Fotheringham, 1976; Bertness, 1981). This study investigates how the sizes and shapes of *Pagurus longicarpus* hermit crabs vary depending on the sizes and shapes of the inhabited shells.

P. longicarpus exhibits geographic variation along the Atlantic coast of North America (*e.g.*, Tables II and VI, Fig. 1). Southern individuals from South and North Carolina tend to be smaller, have relatively longer claws, and exhibit greater right/left claw asymmetry than northern individuals from New Jersey, Long Island Sound, and Massachusetts. The morphological variation of *P. longicarpus* is correlated with differences in the sizes and shapes of the shells used in the different geographic areas. Further, these geographic differences in shell use are due partly to the introduced gastropod *Littorina littorea*. This snail is common in Massachusetts and Long Island Sound, rare in New Jersey, and absent in the Carolinas (Vermeij, 1978, 1982).

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Abbreviations: ASL = anterior shield length, ASW = anterior shield width, RCL = right cheliped length, RPL = right propodus length, RPW = right propodus width, LPL = left propodus length.

[1] Present address: Division of Environmental Research, The Academy of Natural Sciences, 19th and the Parkway, Philadelphia, Pennsylvania 19103.

Materials and Methods

Field sampling

Samples (Table I) were collected at low tide from the low intertidal zone; to avoid biases every individual within a given area was collected. (Sample area varied depending on the density of the hermit crabs.) Samples were preserved in formalin, and each crab's anterior shield length (ASL) was measured using a dissecting microscope equipped with an ocular micrometer. The ASL is the length of the hard part of the carapace and correlates with total carapace length and body weight (Blackstone, 1984). The length (at maximum parallel to the columellar axis) and the width (at maximum perpendicular to the columellar axis) of each crab's shell was measured using a hand caliper. While factor analysis has been used to characterize the shell resource in hermit crabs (Kuris and Brody, 1976), geographic differences in the shell resource of *P. longicarpus* can be seen by using $\frac{1}{2}$ (shell length + shell width) to estimate shell size and shell length/shell width to estimate shell shape (*cf.*, Gould, 1977).

Lab experiments

In September, 1980, small adult *Pagurus longicarpus* from Beaufort, North Carolina, (n = 67) and Guilford, Connecticut (*i.e.*, Long Island Sound) (n = 98) were collected, isolated in fiberglass mesh aquarium compartments (1 crab per compartment), and raised under constant conditions (temperature = 16°C., photoperiod = 12 hours light/12 hours dark, salinity = 30‰, pH = 8.0) for over three years. The Beaufort sample was taken from an intertidal site; the Guilford sample was taken from an intertidal aggregation of very small crabs.

Each isolated individual was fed every two days during the first year and every three days thereafter. At each feeding each individual was fed to excess with fresh or frozen mussels or occasionally one of several commercial fish foods. Crabs also fed extensively on algae growing on the fiberglass mesh, on detritus which accumulated

Table I

Sites and dates of collections of geographic samples

Site	Date	n
Nahant, Massachusetts	29 August 1981	136
	31 August 1982	88
Woods Hole, Massachusetts	28 August 1982	122
Guilford, Connecticut	July–September 1980	664
	July–September 1981	299
	11 September 1982	166
Cold Spring Harbor, New York	4 September 1982	146
Barnegat Bay, New Jersey	17 August 1980	148
	20 September 1981	102
	7 August 1982	75
Beaufort, North Carolina	20 September 1980	139
	22 August 1982	156
Topsail Inlet, North Carolina	21 August 1982	114
Carolina Beach, North Carolina	19 August 1982	85
Southport, North Carolina	19 August 1982	136
Little River, South Carolina	18 August 1982	165
Murrell's Inlet, South Carolina	17 August 1982	86
Pawley's Island, South Carolina	16 August 1982	79

in the sandy substrata, and, by climbing the mesh to the surface, on surface zooplankton using the characteristic surface-feeding behavior described by Scully (1978). The isolation of the individuals did not permit courtship and mating.

Each isolated individual was assigned to a shell treatment and given shells accordingly (see below). As individuals molted and grew each molt of each individual was removed, dried, and stored, forming a permanent record of each individual's growth (*cf.*, Fotheringham, 1976). Crabs were sexed from their molts (the female gonopore is at the third pereiopod base; sex reversal does not occur). Morphometric data were collected from these molts using a dissecting microscope equipped with an ocular micrometer. Final size was judged by a crab's ASL at the time of its death. (A few individuals died in less than a year and were excluded from the comparisons.) Measurements of the right claw seemed most likely to detect shape differences between crabs of the different shell treatments, since in many hermit crab species this claw exhibits clear "fittedness" to inhabited shells (*e.g.*, Benedict, 1900, Hay and Shore, 1918, Edmondson, 1946). Hence, shape comparisons were made by regressing right cheliped length (RCL; the total length of the major claw) on body size (ASL), by regressing right propodus length (RPL; the length of the last segment or chela of the right cheliped) on body size (ASL), and by regressing right propodus length (RPL) on width (RPW). In males, two additional shape comparisons were made. Right/left symmetry of the chelae was measured by regressing right propodus length (RPL) on left propodus length (LPL). Body shape was measured by regressing anterior shield width (ASW) on length (ASL). These bivariate shape relationships are allometric, and regressions of the natural logarithms of the variables allows comparing relative growth rates.

Three shell treatments were used to test the effects of shells on the 165 isolated individuals. These treatments paralleled the geographic differences in shell use (see Table II and Fig. 1): small, high-spired shells *versus* large, low-spired shells. For the high-spired treatment, crabs collected in high-spired shells in the field (*Nassarius vibex* at Beaufort and *Nassarius trivittatus* at Guilford) were offered several properly fitting shells of *Ilyanassa obsoleta*. At each molt, several larger shells were offered. When the crabs outgrew the maximum size shells of *I. obsoleta*, shells of the similar-shaped but larger *Urosalpinx cinerea* were offered up to its maximum size. (This treatment is hereafter referred to as the *U. cinerea* treatment.)

For the low-spired treatment, Beaufort crabs (necessarily collected in high-spired shells) were offered *Littorina littorea* shells. Those that switched into these shells were confined to them by immediate removal of the vacated original shell. Those that did not switch were used in the high-spired treatment. This procedure was employed because removing hermit crabs from their shells requires heat; this might affect development (Waddington, 1954). This problem did not arise with Guilford crabs, for here low-spired shells (*Littorina* species) were occupied by some of the small crabs collected in the field; these crabs were given shells of *Littorina littorea*. Both the Beaufort and Guilford crabs in this treatment were offered *L. littorea* shells up to the maximum size of this species.

A second low-spired treatment was done with shells of *Polinices duplicatus*. The methodology employed here was similar to that used for the Beaufort *L. littorea* treatment. Crabs were offered *P. duplicatus* shells; if they switched, they were included in this shell treatment. (Few small crabs would switch to *P. duplicatus* shells.)

After two years, shell-switching tests were carried out with the Guilford males used in the above experiments. Males inhabiting maximum-size *U. cinerea* shells were divided into two groups. One group was left in the *U. cinerea* shells, while the other was offered shells of *L. littorea* up to the maximum size. Males inhabiting

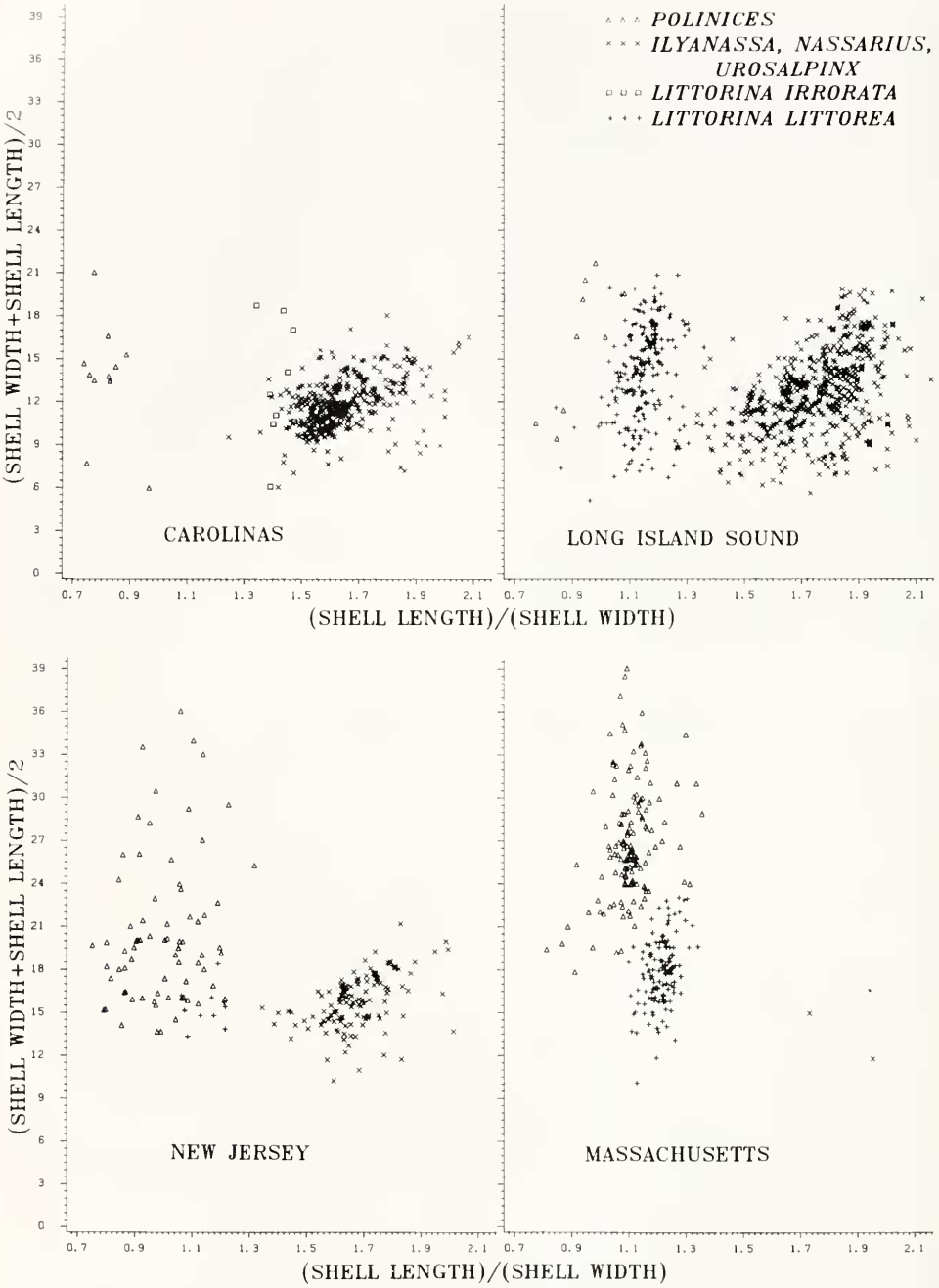

FIGURE 1. For shells inhabited by male *Pagurus longicarpus*, ½ (shell length + width) approximates shell size and shell length/shell width approximates shell shape; these measures are plotted for shells inhabited in North and South Carolina, Long Island Sound, New Jersey, and Massachusetts. Symbols correspond to the indicated shell species. For easier display, seldom used shell species and the very high-spired shells of *Terebra dislocata* (inhabited in the Carolinas) are excluded. Northern crabs inhabit larger, lower-spired shells. When present, *Littorina littorea* shells bridge the gap in the native shell resource between small, high-spired shells and larger, lower-spired shells.

maximum-size *L. littorea* shells were also divided into two groups. One group was left in the *L. littorea* shells, and the other was offered *P. duplicatus* shells.

For all crabs, maximum shell size was estimted by ½ (shell length + shell width) of the final occupied shell. Also, measures of the aperture length (at maximum parallel to the aperture lip, excluding the siphonal notch if present), the aperture width (at maximum perpendicular to the aperture length), the length, and the width for a haphazard sample of the shells used in the experiment were taken. Regressing aperture length on aperture width and length on width provided estimates of shell shape. Shells used in the experiments were collected from Guilford, Connecticut, intertidal areas containing many empty shells.

RESULTS

Field results

Table II compares the geographic data from South and North Carolina, New Jersey, Long Island Sound, and Massachusetts. Northern crabs are larger and inhabit larger and lower-spired shells than southern crabs. Long Island Sound crabs are stunted as are some other invertebrate taxa in this area (W. D. Hartman, pers. comm.). These data agree with those from other studies (South Carolina, Young, 1979; North Carolina, Mitchell, 1975, Kellogg, 1971, 1976; Rhode Island, Scully, 1979).

TABLE II

Regional differences in Pagurus longicarpus *size, utilized shell size, and utilized shell shape (all measures in mm)*

Sex	Crab size[1] mean ± S.D.	Shell size[2] ½(length + width) mean ± S.D.	Shell shape[3] length/width mean ± S.D.	n
		Southern, South and North Carolina		
Males	2.47 ± 0.58	12.37 ± 2.77	1.88 ± 0.68	408
Females	2.34 ± 0.40	12.04 ± 2.92	1.96 ± 0.75	552
		Northern, New Jersey		
Males	4.22 ± 0.84	17.67 ± 4.29	1.41 ± 0.35	208
Females	3.32 ± 0.34	14.85 ± 1.69	1.65 ± 0.11	117
		Northern, Long Island Sound		
Males	2.88 ± 0.72	12.95 ± 3.38	1.54 ± 0.33	817
Females	2.32 ± 0.45	10.89 ± 2.58	1.62 ± 0.29	427
		Northern, Massachusetts		
Males	5.27 ± 1.27	22.66 ± 6.01	1.16 ± 0.11	268
Females	3.82 ± 0.65	15.69 ± 1.77	1.24 ± 0.14	79

[1] Northern crabs (except Long Island Sound females) are larger than southern crabs ($P < 0.0001$ Wilcoxon Rank Sum).

[2] Northern shells (except those of Long Island Sound crabs) are larger than southern shells ($P < 0.0001$ Wilcoxon Rank Sum).

[3] Northern shells are lower spired than southern shells ($P < 0.0001$ Wilcoxon Rank Sum).

Lab results

Size. There are some differences between the initial sizes of the crabs assigned to the shell treatments (Table III). Beaufort females assigned to *L. littorea* and *P. duplicatus* shells are larger than those assigned to *U. cinerea* shells, while Guilford males assigned to *P. duplicatus* shells are larger than those assigned to the other two shells. These non-random assignments occur in cases where the individuals were able to select their shell treatment. Apparently, smaller crabs have a stronger preference for high-spired shells than larger crabs. This is also shown by shell preference studies (Mitchell, 1975; Blackstone, 1984; Blackstone and Joslyn, 1984).

Because of these differences in initial sizes, both the growth increment data and the final size data should be used to judge the differences between shell treatments. In all cases, the crabs in *L. littorea* shells grew more than those in *U. cinerea* shells. The small sample sizes of crabs in *P. duplicatus* shells hamper comparisons to the other shell treatments, but in the case of the Guilford crabs, those in *P. duplicatus* grew significantly more than those in the other shells. There are no significant differences in the lifespans of crabs grown in the different shells.

The shell-switching experiments provided similar data (Table III). Guilford males raised in *U. cinerea* shells, then offered *L. littorea* shells attained larger sizes than males held in *U. cinerea* shells. Guilford males raised in *L. littorea* shells and offered

TABLE III

Sizes of Pagurus longicarpus *raised in three shell types (all measures in mm)*

Location	Sex	Shell	n	Initial size (mean ASL ± S.D.)	Final size (mean ASL ± S.D.)	Growth[1] (mean ± S.D.)	Days[2] (mean ± S.D.)
Beaufort	F	*Urosalpinx*	21	2.32 ± 0.25	4.28 ± 0.32	1.96 ± 0.37	877 ± 368
		Littorina	19	2.46 ± 0.19	5.05 ± 0.60	2.58 ± 0.64	1018 ± 393
		Polinices	1	2.90	5.00	2.10	542
	ANOVA[3] *P*=			0.02	<0.0001	0.002	0.30
Guilford	F	*Urosalpinx*	26	1.88 ± 0.26	4.55 ± 0.42	2.67 ± 0.57	1174 ± 332
		Littorina	24	1.88 ± 0.28	5.21 ± 0.40	3.34 ± 0.50	1245 ± 219
		Polinices	5	2.02 ± 0.26	6.00 ± 0.19	3.98 ± 0.43	1335 ± 47
	ANOVA *P*=			0.53	<0.0001	<0.0001	0.40
Beaufort	M	*Urosalpinx*	10	2.64 ± 0.40	5.61 ± 0.24	2.97 ± 0.48	606 ± 185
		Littorina	11	2.43 ± 0.46	6.10 ± 0.93	3.67 ± 0.92	669 ± 347
		Polinices	4	2.83 ± 0.51	6.45 ± 0.96	3.63 ± 1.10	492 ± 151
	ANOVA *P*=			0.28	0.13	0.13	0.53
Guilford	M	*Urosalpinx*	8	1.81 ± 0.18	5.62 ± 0.64	3.81 ± 0.68	1078 ± 369
		Littorina	13	1.75 ± 0.25	6.44 ± 0.55	4.69 ± 0.63	1108 ± 287
		Polinices	7	2.03 ± 0.17	8.27 ± 0.83	6.24 ± 0.87	1005 ± 231
	ANOVA *P*=			0.04	<0.0001	<0.0001	0.74
Guilford[4]	M	U/U	6	5.33 ± 0.28	5.88 ± 0.50	0.55 ± 0.28	642 ± 142
		U/L	8	5.51 ± 0.36	6.45 ± 0.39	0.94 ± 0.51	606 ± 212
	ANOVA *P*=			0.34	0.03	0.12	0.73
		L/L	9	6.07 ± 0.42	6.68 ± 0.42	0.61 ± 0.31	585 ± 158
		L/P	7	6.30 ± 0.29	7.51 ± 0.82	1.21 ± 0.57	558 ± 221
	ANOVA *P*=			0.23	0.02	0.02	0.79

[1] Total growth increment.
[2] Days from first molt until death.
[3] ANOVA of the three shell treatments: *P* is the probability that the treatments are the same.
[4] Shell-switching experiments: U/U = *Urosalpinx* to *Urosalpinx* (control), U/L = *Urosalpinx* to *Littorina* (test), L/L = *Littorina* to *Littorina* (control), L/P = *Littorina* to *Polinices* (test).

P. duplicatus shells grew more and attained larger sizes than males held in *L. littorea* shells.

For final shell size, Table IV shows that *P. duplicatus* shells are significantly larger than shells of the two other species, but *L. littorea* shells are not significantly larger than *U. cinerea* shells. It may be that shell-type affects crab growth and size (see Bertness, 1981).

Individuals from the same locality and shell treatment varied in final size (see standard deviations in Table III). In the *U. cinerea* and *L. littorea* shell treatments, the crabs outgrew the largest shells available, and there were slight differences among individuals in the sizes of their final shells (see standard deviations in Table IV). But Table V shows that there is no within-shell treatment correlation between final crab size and final shell size in these shell treatments. A correlation is present with the *P. duplicatus* treatments, but this likely results from the preferences of the individuals; in this treatment larger shells were always available.

Shape. Table VI shows bivariate regressions of the log-transformed data from the molts of the lab-grown individuals. The slope of each regression represents rate at which the shape relationship between the two variables changes throughout the ontogeny (Huxley, 1932; Gould, 1966). A slope greater than unity indicates that the body part represented by the dependent variable grows relatively faster than the body part represented by the independent variable. In terms of actual shape, the body part represented by the dependent variable would become relatively longer throughout the ontogeny. A slope less than unity indicates that the dependent variable grows relatively slower than the independent variable; thus that body part would become relatively shorter throughout the ontogeny. A slope equal to unity entails no relative growth differences between the parts in question and no shape changes during the ontogeny.

The data of Table VI show a number of general patterns. First, there are regularities of growth which have been found in other hermit crabs (Bush, 1930) and other decapod crustaceans (Huxley, 1932), *e.g.*, the right claw (RCL) grows faster than the body (ASL), and in most cases the chela of the right claw (RPL) grows relatively still faster. Second, there are differences between the sexes, and the males show greater relative growth of the claws (this is also true of other decapods, see Bush, 1930;

TABLE IV

Final shell size (in mm) of male Pagurus longicarpus *raised in three shell species*

Location	Shell	n	Final shell size ½(length + width) mean ± S.D.	ANOVA[1] *P* =	Pairwise *t*-tests[2] *P* = U	L	P
Beaufort	*Urosalpinx*	10	21.43 ± 0.46	0.0001	—	0.74	0.0001
	Littorina	11	21.57 ± 0.85			—	0.0001
	Polinices	4	26.98 ± 1.74				—
Guilford	*Urosalpinx*	8	21.04 ± 0.68	0.0001	—	0.23	0.0001
	Littorina	13	21.95 ± 1.21			—	0.0001
	Polinices	7	28.74 ± 2.85				—

[1] ANOVA of the three shells: *P* is the probability that the shells are the same size.

[2] Paired *t*-tests: U = *Urosalpinx*, L = *Littorina*, P = *Polinices*, *P* is the probability that the pair of means is the same; thus, *P* = 0.74 that the means of the Beaufort *Urosalpinx* and *Littorina* treatments are the same, etc.

TABLE V

Within shell treatment correlation of final shell and crab size in male Pagurus longicarpus *raised in three shell species*

Location	Shell	Regression[1]	n	R^2	Significance level F	*P*
Beaufort	*Urosalpinx*	Y = −0.09X + 7.45	10	0.03	0.22	0.65
	Littorina	Y = 0.27X + 0.31	11	0.07	0.68	0.43
	Polinices	Y = 0.53X − 7.73	4	0.91	19.76	0.05
Guilford	*Urosalpinx*	Y = 0.31X − 0.80	8	0.10	0.70	0.43
	Littorina	Y = 0.08X + 4.58	13	0.03	0.39	0.54
	Polinices	Y = 0.27X + 0.65	7	0.83	24.39	0.004

[1] Y = crab anterior shield length, X=½(shell length + width).

Huxley, 1932). Third, there are consistent differences between the Beaufort and Guilford crabs, and the latter exhibit reduced relative growth.

There are also differences among the shell treatments. Guilford males show clear trends. Regressing RCL on ASL shows that males in *U. cinerea* shells have a higher rate of right claw growth relative to body growth than do males in *L. littorea* and *P. duplicatus* shells. Males in *L. littorea* shells have an intermediate rate, but this rate is not significantly higher than the rate of males in *P. duplicatus* shells. (As with the size comparisons, shape comparisons of crabs in *P. duplicatus* shells are hampered by small sample sizes.) Regressing RPL on ASL shows that males in *U. cinerea* shells have a higher rate of right chela growth relative to body growth than do males in *L. littorea* and *P. duplicatus* shells. Males in *L. littorea* shells again have an intermediate rate. Regressing RPL on LPL shows that males in *U. cinerea* shells have a higher rate of right chela growth relative to left chela growth than do males in *L. littorea* and *P. duplicatus* shells. Males in *L. littorea* shells have an intermediate rate. Regressing ASW on ASL shows that males in *U. cinerea* shells have a higher rate of body width growth relative to body length growth than do males in *L. littorea* and *P. duplicatus* shells. (Males in *U. cinerea* shells exhibit a slightly positively allometric rate, while those in *L. littorea* and *P. duplicatus* shells exhibit a slightly negatively allometric rate.) Finally, regressing RPL on RPW shows that males in *U. cinerea* shells have the same rate of right chela length growth relative to right chela width growth as do males in *L. littorea* and *P. duplicatus* shells.

These differences in relative growth rate translate into differences in shape. Males in *U. cinerea* shells have longer claws, greater right/left asymmetry of claws, and wider bodies than males in *L. littorea* and *P. duplicatus* shells, while males in *L. littorea* shells are intermediate in shape.

Guilford males used in the shell-switching experiments show shape changes which parallel these between shell treatment differences. Table VII shows the results from crabs raised in *L. littorea* shells and then either held in these shells or offered *P. duplicatus*. Regression of RCL or RPL on ASL show that for the control crabs the rate of right claw growth relative to body growth decreases, but not significantly, while for the test crabs this rate decreases significantly.

Overall, the patterns seen in Guilford males apply to Beaufort males, though some differences exist, possibly because of the smaller sample sizes: (1) while differences in the rate of cheliped growth (RCL regressed on ASL), chela growth (RPL regressed on ASL), and right/left chela growth (RPL regressed on LPL) show the same polarity

as in the Guilford males, these differences are not significant in all comparisons, (2) the rate of body width relative to body length growth (ASW regressed on ASL) shows no significant differences between shell treatments, and (3) the rate of claw length relative to width growth (RPL regressed on RPW) shows slight differences between shell treatments and males in *L. littorea* have a faster rate than males in the other shells.

Females show a different pattern than males. Except for very slight differences in the *P. duplicatus* treatment (which are likely due to sampling biases), Guilford females do not show among shell differences in the rates of shape changes of the variables measured. Beaufort females show insignificant differences in the rates of claw growth (RCL or RPL regressed on ASL) and show significant differences in the rates of claw length relative to width growth (RPL regressed on RPW). As with the Beaufort males, females in *L. littorea* shells have a faster rate than those in *U. cinerea* shells.

Table VIII presents the data on the aperture shape (aperture length regressed on width) and shell shape (length regressed on width) of the sample of shells used in the experiments. Shells used in the high-spired treatment (*I. obsoleta* and *U. cinerea*) are long and narrow with long, narrow apertures. *L. littorea* shells are short and wide with short, wide apertures. *P. duplicatus* shells are very short and wide, but have somewhat long apertures.

Discussion

Markham (1968) and Fotheringham (1976) show that hermit crabs given larger shells attain larger sizes than those given small shells. Drapkin (1963) makes similar statements, but does not present quantitative data. Bertness (1981) shows that the type of shell inhabited by a hermit crab can influence its growth. The data presented here agree with the results of these workers. These data also show that a hermit crab can continue to grow once its shell has become too small. For instance, the control males in the shell-switching experiments were too large for their shells at the onset of the experiment, but continued to grow (see Table III), albeit more slowly than crabs given shells which favored growth.

These data also provide insight into whether hermit crabs are morphologically molded by their inhabited shells. Goldschmidt (1940) summarized evidence to support this idea. Much of this evidence, however, has been discredited (for instance, see discussion in Wolff, 1961). Further, Thompson (1904) concluded that hermit crabs could not be molded by their inhabited shells. Nevertheless, the molding hypothesis is still suggested by some (*e.g.*, see Elwood *et al.*, 1979).

If the molding hypothesis is correct, the shape of a crab should change with growth to better conform to the shape of its inhabited shell. Both aperture shape and total shell shape would affect the crabs' shape. Long, narrow, highly asymmetric shells with long, narrow apertures present a crab with a living space which is elliptical in circumference, long in length, and oriented asymmetrically. Shorter, wider, more symmetric shells with rounder apertures present a crab with a living space which is more circular in circumference, shorter in length, and oriented more symmetrically. Thus crabs which inhabited *I. obsoleta* and *U. cinerea* shells should develop longer and more asymmetric appendages and flatter, wider bodies than those which inhabited *L. littorea* or *P. duplicatus* shells. Additionally, the right chela, which serves as an operculum, should be molded to fit the aperture shape; crabs in *I. obsoleta* and *U. cinerea* shells should have long, narrow chelae, while those in *L. littorea* and *P. duplicatus* shells should have shorter, wider chelae.

TABLE VI

Shape regressions of molts of Pagurus longicarpus *raised in three shell types*

Variables[1]	Shell[2]	Regression	Molts	R^2	ANCOVA[3] $P =$	Orthogonal contrasts[4] *Littorina* $P=$	Orthogonal contrasts[4] *Polinices* $P=$
			Beaufort males				
X = log(ASL)	U	Y = 1.48X + 0.98	85	0.98	0.0002	0.03	0.002
Y = log(RCL)	L	Y = 1.39X + 1.07	115	0.98	—	—	0.06
	P	Y = 1.30X + 1.19	30	0.99	—	—	—
X = log(ASL)	U	Y = 1.47X + 0.01	85	0.98	0.001	0.66	0.008
Y = log(RPL)	L	Y = 1.44X + 0.03	115	0.98	—	—	0.008
	P	Y = 1.31X + 0.20	30	0.99	—	—	—
X = log(LPL)	U	Y = 1.38X − 0.06	81	0.98	0.0001	0.0001	0.001
Y = log(RPL)	L	Y = 1.28X + 0.11	114	0.99	—	—	0.88
	P	Y = 1.27X + 1.12	30	0.99	—	—	—
X = log(RPW)	U	Y = 1.27X + 0.60	85	0.97	0.0005	0.04	0.49
Y = log(RPL)	L	Y = 1.34X + 0.51	115	0.98	—	—	0.03
	P	Y = 1.19X + 0.64	30	0.98	—	—	—
X = log(ASL)	U	Y = 1.00X + 0.05	85	0.99	0.08	0.12	0.98
Y = log(ASW)	L	Y = 0.98X + 0.08	114	0.99	—	—	0.23
	P	Y = 1.00X + 0.05	33	0.99	—	—	—
			Guilford males				
X = log(ASL)	U	Y = 1.37X + 1.07	189	0.99	0.0001	0.0007	0.0002
Y = log(RCL)	L	Y = 1.31X + 1.12	273	0.99	—	—	0.18
	P	Y = 1.25X + 1.15	99	0.99	—	—	—
X = log(ASL)	U	Y = 1.42X + 0.02	189	0.99	0.0001	0.0001	0.0001
Y = log(RPL)	L	Y = 1.35X + 0.09	273	0.99	—	—	0.005
	P	Y = 1.27X + 0.16	98	0.99	—	—	—
X = log(LPL)	U	Y = 1.25X + 0.10	186	0.99	0.0001	0.002	0.0001
Y = log(RPL)	L	Y = 1.22X + 0.14	269	0.99	—	—	0.03
	P	Y = 1.18X + 0.18	99	0.99	—	—	—
X = log(RPW)	U	Y = 1.14X + 0.69	189	0.98	0.95	0.93	0.39
Y = log(RPL)	L	Y = 1.13X + 0.69	273	0.99	—	—	0.33
	P	Y = 1.13X + 0.67	99	0.99	—	—	—
X = log(ASL)	U	Y = 1.01X + 0.04	187	0.99	0.0001	0.006	0.0002
Y = log(ASW)	L	Y = 0.98X + 0.06	264	0.99	—	—	0.07
	P	Y = 0.97X + 0.08	97	0.99	—	—	—
			Beaufort females				
X = log(ASL)	U	Y = 1.19X + 1.19	226	0.97	0.18	0.28	0.57
Y = log(RCL)	L	Y = 1.16X + 1.22	218	0.98	—	—	0.72
	P	Y = 1.12X + 1.27	8	0.99	—	—	—
X = log(ASL)	U	Y = 1.23X + 0.16	226	0.95	0.15	0.17	0.19
Y = log(RPL)	L	Y = 1.20X + 0.20	218	0.98	—	—	0.29
	P	Y = 1.08X + 0.35	8	0.99	—	—	—
X = log(RPW)	U	Y = 1.01X + 0.74	226	0.97	0.0001	0.006	0.45
Y = log(RPL)	L	Y = 1.08X + 0.69	218	0.97	—	—	0.20
	P	Y = 0.96X + 0.81	8	0.99	—	—	—
			Guilford females				
X = log(ASL)	U	Y = 1.11X + 1.25	396	0.98	0.77	0.47	0.62
Y = log(RCL)	L	Y = 1.10X + 1.26	364	0.99	—	—	0.93
	P	Y = 1.10X + 1.26	80	0.98	—	—	—

TABLE VI (*Continued*)

Variables[1]	Shell[2]	Regression	Molts	R^2	ANCOVA[3] $P =$	Orthogonal contrasts[4] *Littorina* $P=$	Orthogonal contrasts[4] *Polinices* $P=$
		Guilford females					
X = log(ASL)	U	Y = 1.15X + 0.19	396	0.98	0.80	0.15	0.43
Y = log(RPL)	L	Y = 1.15X + 0.22	366	0.98	—	—	0.97
	P	Y = 1.14X + 0.22	81	0.98	—	—	—
X = log(RPW)	U	Y = 1.02X + 0.70	396	0.99	0.57	0.70	0.01
Y = log(RPL)	L	Y = 1.02X + 0.70	367	0.99	—	—	0.007
	P	Y = 1.01X + 0.74	81	0.99	—	—	—

[1] ASL = anterior shield length, LPL = left propodus length, RPW = right propodus width, RCL = right cheliped length, RPL = right propodus length, ASW = anterior shield width.

[2] U = *Urosalpinx*, L = *Littorina*, P = *Polinices*.

[3] ANCOVA tests for homogeneity of slopes between the three shell treatments: *P* is the probability that the slopes are the same; thus, for log(RCL) regressed on log(ASL) for Beaufort males, $P = 0.0002$ that the slopes of the *Urosalpinx*, *Littorina*, and *Polinices* regressions are the same, etc.

[4] Orthogonal contrasts between indicated pairs of shell treatments: *P* is the probability that the treatments are the same; thus, for log(RCL) regressed on log(ASL) for Beaufort males, $P = 0.03$ that the *Urosalpinx* and *Littorina* treatments are the same; $P = 0.002$ that the *Urosalpinx* and *Polinices* treatments are the same, etc.

In some ways, the data presented here agree with these predictions. Male crabs raised in *U. cinerea* shells did grow relatively longer chelipeds, longer chelae, and greater right/left asymmetry of chelae than those raised in *L. littorea* or *P. duplicatus* shells. Also, the Guilford males in *U. cinerea* shells grew wider bodies (ASW regressed on ASL) than the other crabs. The growth of the right chela (RPL regressed on RPW), however, does not conform to the predictions of the molding hypothesis. In Guilford males, crabs in *U. cinerea* shells do not grow narrower chelae than crabs in *L. littorea* or *P. duplicatus* shells. In Beaufort males, crabs in *L. littorea* shells grew narrower chelae than crabs in *U. cinerea* shells. This is surprising in view of the tendency for

TABLE VII

Shape regressions of molts of Guilford male Pagurus longicarpus *used in the shell-switching experiments*

Original shell/test shell[1]		Regression	Molts	R^2	ANCOVA[2] F	ANCOVA[2] *P*
		X = log(anterior shield length), Y = log(right cheliped length)				
Littorina/Littorina	Before	Y = 1.32X + 1.12	108	0.99	0.75	0.39
	After	Y = 1.22X + 1.27	39	0.66		
Littorina/Polinices	Before	Y = 1.33X + 1.09	77	0.99	9.90	0.002
	After	Y = 1.09X + 1.50	32	0.90		
		X = log(anterior shield length), Y = log(right propodus length)				
Littorina/Littorina	Before	Y = 1.36X + 0.09	108	0.99	2.33	0.13
	After	Y = 1.17X + 0.41	39	0.61		
Littorina/Polinices	Before	Y = 1.36X + 0.07	77	0.99	8.48	0.004
	After	Y = 1.12X + 0.48	32	0.87		

[1] For each group, regressions are presented for rate before and after shells were switched.

[2] ANCOVA test for homogeneity of slopes: *P* is the probability that the before and after slopes are the same.

TABLE VIII

Shape regressions from a sample of the shells used to raise Pagurus longicarpus

Shell species[1]	n	Aperture shape[2] Regression	R^2	Shell shape[3] Regression	R^2
Ilyanassa obsoleta	164	$Y_1 = 2.15X_1 + 0.29$	0.93	$Y_2 = 2.14X_2 - 3.33$	0.96
Urosalpinx cinerea	92	$Y_1 = 1.62X_1 + 1.53$	0.64	$Y_2 = 1.59X_2 + 3.55$	0.75
Littorina littorea	229	$Y_1 = 1.20X_1 + 1.35$	0.90	$Y_2 = 1.15X_2 + 0.13$	0.96
Polinices duplicatus	85	$Y_1 = 1.41X_1 + 0.70$	0.99	$Y_2 = 0.96X_2 - 1.36$	0.96

[1] The first two species constituted the high-spired treatment.
[2] X_1 = aperture width, Y_1 = aperture length.
[3] X_2 = shell width, Y_2 = shell length.

globose shell-living hermit crabs to have wide, operculate chelae (*e.g., Pagurus pollicaris, Coenobita compressus, Calcinus obscurus,* for other examples see Benedict, 1900, Hay and Shore, 1918, Edmondson, 1946).

Further problems with the molding hypothesis are apparent when males in *L. littorea* and *P. duplicatus* shells are compared. The latter shell is somewhat more globose and low-spired than the former but the shape differences are not as dramatic as those between *L. littorea* and *U. cinerea* shells (Table VIII). However, males in *P. duplicatus* shells differ as much in relative cheliped growth (RCL regressed on ASL), relative chela growth (RPL regressed on ASL), and right/left chela growth (RPL regressed on LPL) from males grown in *L. littorea* shells as these males differ from those grown in *U. cinerea* shells (Table VI).

The data from female *P. longicarpus* are inconsistent with the molding hypothesis. In Guilford females, shell shape has no effect on relative cheliped growth (RCL regressed on ASL), on relative chela growth (RPL regressed on ASL), or on the growth of the right chela (RPL regressed on RPW). In Beaufort females, the only significant effect is on the growth of the right chela, and the differences are the opposite of those expected from the molding hypothesis (crabs raised in *L. littorea* shells grow narrower chelae than crabs in *U. cinerea* shells).

The variation between the sexes suggests another explanation for the differences in claw length between males of the different shell treatments. Male hermit crabs fight for mates and large males succeed more than small males (see Hazlett, 1981; this is particularly true of *Pagurus longicarpus,* Thompson, 1904, and pers. obs.). It may be that small-shelled males which are unable to grow large in absolute size, compensate by growing a relatively longer right claw. Since the right claw is the main instrument of combat (*e.g.,* see Reese, 1983), males with a relatively longer claw might be more successful than those with a shorter claw. Selection may have favored a growth program in males in which stunting in size results in increased relative growth of the right claw.

This sexual selection hypothesis, however, does not explain why the Beaufort females should show greater differences in shape between shell treatments than the Guilford females (Table VI). A final hypothesis can explain these differences as well as the differences between the sexes. Size, shape, and developmental timing are interrelated phenomena not only evolutionarily (*e.g.,* Gould, 1977; Bonner and Horn, 1982) but developmentally as well. Vermeij (1980) summarizes the results of field studies which show this interrelationship in gastropods. Generally, slower growth correlates with smaller final size and faster relative growth. A field experiment by

Kemp and Bertness (1984) supports these findings. They grew *Littorina littorea* snails under crowded and less crowded conditions. The crowded snails grew more slowly and exhibited increased negative allometry. (The slopes of the double logarithmic regressions were all less than unity, and the crowded snails had reduced slopes as compared to the normal snails.) These results are similar to those presented here. In both cases, stunting individual's growth rates through unfavorable environmental conditions (crowding in the case of the snails, small shells in the case of the hermit crabs) resulted in slower total growth of the body, but more rapid relative growth (= change in body shape). The hermit crab results would further suggest that the greater the degree of allometry the greater the effects of stunting. Males have greater positive allometry than females (Bush, 1930; Huxley, 1932; Table VI) and hence display greater differences between shell treatments. Beaufort females have greater positive allometry than Guilford females (Table VI) and hence display more similarity to the males.

The results of Ray (1960) are somewhat different. Working with a number of taxa, Ray grew individuals at low and high temperatures. At low temperatures individuals grew more slowly, exhibited reduced positive allometry, and achieved larger final size. The correlation between larger size and reduced allometry is expected and agrees with results presented here. However, the correlation of slower growth with reduced positive allometry differs from results presented here and in Kemp and Bertness (1984). Possibly, there are fundamentally different effects associated with slowed growth caused by slowed metabolic processes as opposed to slowed growth caused by crowding and stunting.

The relationship between body growth rate and relative growth rate needs further clarification. Because the growth of a part is often judged relative to the growth of the body (Huxley, 1932; Gould, 1966; Table VI), a correlation between faster body growth and slower relative growth could be spurious. For instance, regressing RCL on ASL to judge the relative growth of the claw automatically implies that if the growth rate of ASL increases, the relative growth rate of RCL decreases. However, Guilford females in small shells exhibit reduced body growth but no change in relative growth, and male crabs exhibit changes in the growth of the chelae relative to each other (RPL regressed on LPL). The inverse relationship between body growth and relative growth is more than just a simple mathematical tautology; rather, this interaction indicates the existence of underlying developmental mechanisms. Perhaps negative feedback systems controlling growth act to maintain specific relationships between body growth and relative growth (*cf.*, Stebbing and Heath, 1984).

Laird *et al.* (1968) and Barton and Laird (1969) propose that allometry is the result of temporal, not spatial, growth gradients. This suggests that hermit crabs in small shells exhibit an accelerated growth program. Perhaps as the small shell causes premature curtailment of normal body growth, homeostatic feedback mechanisms cause premature acceleration of normal appendage growth. Thus a small crab is produced with the shape that would normally be found in a large crab, *i.e.*, longer appendages and greater right/left asymmetry.

The interrelationship of growth rate, relative growth, and final size is of significance to a mechanistic understanding of general processes of growth and form. Further experimental manipulation of organisms' environments would doubtless provide additional insight into how these parameters equilibrate during an organism's development. Because hermit crabs are uniquely dependent on the gastropod shells they occupy and because these shells can be easily measured and manipulated, hermit crabs are ideal subjects for further research in this area.

Geographic variation in Pagurus longicarpus

Comparisons of *Pagurus longicarpus* raised in small, high-spired shells and those raised in large, low-spired shells show that the former are smaller than the latter and that males in the former grow relatively longer chelipeds and chelae and greater right/left asymmetry of chelae than males in the latter. These differences may provide insight into the geographic variation of *P. longicarpus*. Southern individuals are smaller and grow relatively longer claws and greater right/left asymmetry of claws than northern individuals (Table II, Table VI). Further, southern individuals inhabit smaller, higher-spired shells than northern individuals (Table II, Fig. 1). It may be that the differences in inhabited shells caused the observed morphological variation in *P. longicarpus*. Three points will be made in this regard:

(1) *Geographic differences are endogenous.* Morphological differences can be induced in individuals of the same geographic population by inhabiting different shell-types. These ecophenotypic differences parallel differences between individuals of the different geographic populations. Nevertheless, individuals from the different geographic populations grown in the same environment in the same shell-type still exhibit differences. Morphological differences between geographic populations thus likely have a genetic basis. If shells were an evolutionary cause for this genetic divergence, mechanisms such as genetic assimilation (Waddington, 1954; Ray, 1960) or selection must be invoked.

(2) *Some geographic differences cannot be induced by shells.* In male *P. longicarpus* chela shape shows clear geographic differences but no induced differences. Further, females show clear geographic differences in cheliped length, chela length, and chela shape, but none of these differences can be induced by shell-type. If shells are the cause of geographic variation, these differences could be explained by pleiotropy (linkage with genes that were assimilated or selected for), additional selection, or genetic drift.

(3) Littorina littorea: *a causal agent?* Raising individuals in large, low-spired shells (*versus* small, high-spired shells) induces differences which parallel some of the differences between northern and southern *P. longicarpus*. *Littorina littorea* is one of the major large, low-spired shells in Massachusetts and Long Island Sound, but is not found at all in the Carolinas (Fig. 1). This shell is a European species which has become common in Massachusetts and Long Island Sound in the last century and a half (Bequaert, 1943; Vermeij, 1978, 1982). In these northern areas, *L. littorea* shells bridge the gap of size and shape between small native shells (*Nassarius, Ilyanassa, Urosalpinx*) and large native shells (*Polinices*). It may be that *L. littorea* shells constitute a significant difference in the shell resource between southern and northern areas. Thus the introduction of *L. littorea* and its displacement of native snails (Brenchley and Carlton, 1983) may have changed the perception of the shell resource by *P. longicarpus*. By inhabiting the introduced shells, crabs grew larger and began to use large native shells as well. Size and shape differences were at first ecophenotypic but were genetically assimilated or selected for. Other shape differences possibly occurred through pleiotropy or additional selection. This scenario must be considered in view of the work of Drapkin (1963) who describes the introduction of a large gastropod to the Black Sea followed by an increase in the size of the native hermit crabs. The presence of a large native littorine, *Littorina irrorata*, and the scarcity of *L. littorea* south of Long Island Sound weaken this hypothesis. On the other hand, *L. irrorata* is a higher-spired shell than *L. littorea*, and does not bridge the gap in the native shell resource (Fig. 1). Also, even in New Jersey, where *L. littorea* is rare, its shells occupy a central position in the shell resource (Fig. 1).

In summary, the data presented here show that there is a close interaction between hermit crabs and inhabited shells during ontogeny and that shell size and shape can have profound effects on crab size and shape. These data suggest that the size and shape spectrum of utilized shells be considered when studying morphological differences in hermit crabs. However, all available evidence should be carefully considered before drawing any causal connections between hermit crab morphology and the morphology of inhabited shells. This is especially true for morphological variation in *P. longicarpus*. While it is possible to make hypotheses concerning the effects of shells, particularly the introduced *L. littorea*, at present such hypotheses are only partially supported by available data. Historical records of *P. longicarpus* must be investigated, alternative hypotheses must be considered, and general processes of growth and development must be further explored.

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